

Genetic Relationships of Sockeye Salmon (*Oncorhynchus nerka*) in the Aniakchak River Drainage, Alaska



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Fig. 1 Study area and Populations

Table 1: Microsatellite Data Collection Summary

Population and Year	Number of genotyped individuals per locus						Averaged across Loci
	One102	One105	One108	One109	One110	One115	
Surprise Lake (SL)							
2001	44	54	53	54	54	51	51.7
2002	42	41	43	43	43	40	42.0
2003	53	53	51	52	49	54	52.0
Population total	86	95	96	97	97	91	145.7
Aniakchak River Above Gates (ARAG)							
2001	18	26	25	28	28	24	27.2
2002	35	43	43	43	41	41	41.0
2003	47	48	46	48	46	48	47.2
Population total	53	69	68	71	69	65	115.4
Albert Johnson Creek (AJC)							
2001	21	29	28	29	29	27	27.2
2002	27	28	34	34	30	25	29.3
2003	52	55	55	56	54	51	53.8
Population total	79	81	89	90	84	76	110.3
Black Lake (BL)							
2002	40	50	48	49	50	45	47.0
2003	40	43	44	43	43	38	41.8
Population total	40	43	44	43	43	38	88.8
Meshik Lake (MESH)							
2003	85	91	91	91	91	91	90.0
Averaged across Pop. years	42.0	46.6	46.8	47.5	46.5	44.6	45.7
Averaged across Pops.	100.8	111.8	112.2	114.0	111.6	107.0	109.6

Table 2: Population Statistics

Population	Sample Size	Loci Typed	Unbiased Hz	Unbiased Hz SD	Obs Hz	Obs Hz SD	No. of Alleles	No. of Alleles SD
SL	151	6	0.809	0.051	0.792	0.014	12.33	5.09
ARAG	120	6	0.806	0.050	0.806	0.015	12.00	3.90
AJC	119	6	0.795	0.059	0.793	0.016	12.83	5.04
BL	95	6	0.826	0.060	0.833	0.016	14.00	5.06
MESH	91	6	0.797	0.043	0.798	0.017	11.33	3.93

Table 3. Pairwise Fst Values

	ARAG	AJC	BL	MESH
SL	0.0112	0.0427	0.0184	0.0409
ARAG		0.0385	0.0200	0.0473
AJC	0.0385		0.0341	0.0570
BL	0.0200	0.0341		0.0375
MESH	0.0473	0.0570	0.0375	

All significant (corrected alpha P<0.008)

Introduction

Sockeye salmon (*Oncorhynchus nerka*) at Aniakchak National Monument and Preserve, Alaska, present an interesting model system to study recent colonization, ecological speciation and life history interactions. The study site is located on the Alaska Peninsula and has had a turbulent geological history (Fig. 1). A massive eruption 3,500 years ago formed a large caldera that filled with water, creating a lake similar to Crater Lake in Oregon (McGimsey et al. 1994). Approximately 1,800 years before the present (bp) the caldera wall gave way resulting in a large flood and the formation of the Aniakchak River, which connects the remainder of the caldera lake (Surprise Lake) with the Pacific Ocean. Subsequent smaller eruptions approximately 500 and 73 bp, as well as others with less certain dates, have also drastically altered the lake and impacted or potentially wiped out any sockeye populations present during that time (Hubbard 1952). The habitat for the sockeye salmon that currently spawn in the Aniakchak Caldera may have been available for colonization as early as 1,800 bp (based on access following the flood) or as recently as 73 bp (based on the timing of the most recent eruption).

Anadromous sockeye employ a variety of life history strategies that can be grouped into two basic categories. The first includes the use of a lake as a nursery where the young stay to rear for 1-2 years after hatching. This contributes to a high rate of growth in an environment with few predators (Burgner 1991). Following this growth period, the sockeye migrate to the sea where they stay for 1-4 years before returning to their natal lake system. Spawning may occur in lake outlets, inlets or near beaches. Due to the advantage of the lake nursery, these lake-type sockeye return to their natal site with great consistency and seldom stray to adjacent areas (Wood 1995). The disadvantage of this life history strategy is that the existence of the nursery lake is often temporary. As the ice sheets advance during the next glacial period, many of the freshwater lakes that served as nursery lakes for sockeye salmon may be lost (Pielou 1994). Many of the lake-type populations of sockeye may effectively be evolutionary dead ends, and therefore, less valuable to the long-term persistence of sockeye salmon in areas of intermittent habitat availability (Wood 1995).

The other life history category does not include a freshwater nursery lake. These sockeye either migrate to the ocean several months (sea-type), or 1-2 years (river-type) after they emerge (Wood et al. 1987). These strategies are both similar in the sense that they are less productive and fish tend to stray more from their natal sites (Eiler et al. 1992). This ability to stray and colonize other areas is of great importance in an evolutionary sense. During a period of glaciation these sea- and river-type populations may persist in refugia. As the glaciers retreat, the straying characteristic of these populations will lead to the recolonization of new habitats and the formation of new spawning populations that evolve to have a lake-type life history (Wood 1995).

Five spawning aggregates of sockeye salmon are important in this study (Fig. 1). The Surprise Lake (SL) population is along the eastern beach of Surprise Lake. These sockeye are lake-type beach spawners. At the lake outlet is a population of lake-type riverine spawning sockeye named Aniakchak River Above Gates (ARAG). The Aniakchak river then tumbles down the volcano in a long series of rapids (1,000 ft of elevation lost in 15 miles) and joins with a substantial tributary, Albert Johnson Creek (AJC). The third spawning aggregate spawns in this tributary and these sockeye are river-type spawners; their juveniles do not have the benefit of access to Surprise Lake for rearing before outmigration to the Pacific Ocean. A fourth population is a large commercially important lake-type population that returns to the Chignik River and spawns in Black Lake (BL). The mouth of the Chignik River is 100 km southwest of the mouth of the Aniakchak River. The fifth population, Meshik Lake (MESH), is geographically proximate to the Albert Johnson Creek but currently has a physical barrier to reproduction as it is across the Alaska Peninsula divide and drains into the Bering Sea. I used microsatellite genetic data to determine the extent of reproductive isolation among these populations.

Unrooted Neighbor Joining Tree

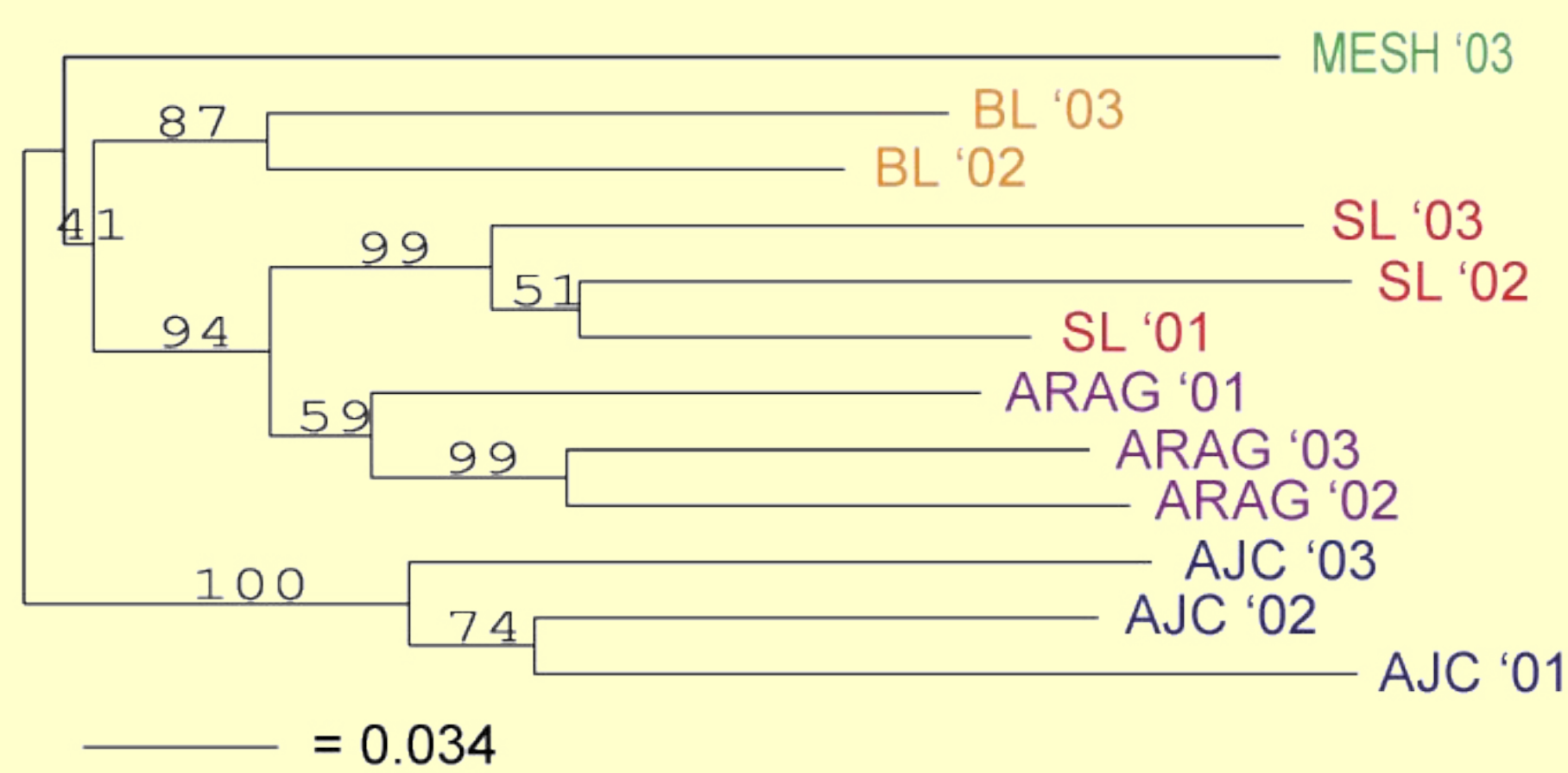


Fig. 2 An unrooted neighbor joining tree based on Cavalli-Sforza and Edwards chord distance. Bootstrap values based on 2000 iterations

Methods

Adult Sample Collection

Genetic sampling of Aniakchak National Monument and Preserve spawning adults took place in early August (2001-2003). The field crew sampled individuals at Surprise Lake from known spawning aggregates along the beach and in the outlet, and at Albert Johnson Creek roughly 2 miles upstream from the confluence with Aniakchak River (Hamon 2001). The Black Lake sockeye were sampled in July (2002-2003) at the Chignik weir by the Alaska Department of Fish and Game. Tissues were stored in ethanol and brought to the laboratory for DNA analyses.

Molecular Data Collection

Total genomic DNA was extracted from the intact fin clips using the Puregene DNA Isolation Kits (Gentra Systems, Inc.). The six microsatellites used in this study are One102, One105, One108, One109, One110, One115 (Olsen et al. 2000). In general, PCR reactions were conducted in 10 µl volumes using approximately 50 ng of genomic DNA, 0.1-0.2 units of Taq DNA polymerase (Perkin Elmer), and buffer (Scribner et al. 1996) for 30-40 cycles. Gel electrophoresis and visualization of microsatellite alleles were performed using LI-COR Model 4200 and IR2 automated fluorescent DNA Sequencers (Middendorf et al. 1992) and sizing was performed using V3.00 Gene ImagIR (LI-COR Lincoln, NE).

Molecular Data Analysis

Genetic data was analyzed using a variety of software from different statistical packages including ARLEQUIN (Schneider et al. 1997), BIOSYS (Swofford and Selander 1981), BOTTLENECK (Piry et al. 1998), CONSENSE and NEIGHBOR from PHYLIP (Felsenstein 1993), and GENEPOP (Raymond and Rousset 1997). Analysis for heterozygosity, genetic disequilibrium, and Fisher's exact tests for Hardy-Weinberg equilibrium (HWE) was tested using GENEPOP. ARLEQUIN (FSTAT pairwise comparisons) were performed to test for differences in allele frequencies between populations and to calculate mean relatedness among populations. Statistical significance of the proportion of shared alleles between populations was tested using the proportion of shared alleles between populations based on Cavalli-Sforza and Edwards chord distance (1967) generated using BIOSYS was plotted as a neighbor-joining (NJ) tree using NEIGHBOR and CONSENSE applications from PHYLIP.

Results

- 576 individuals were genotyped at 6 loci (Tables 1, 2).
- Of 72 tests performed, only 5 were significantly out of Hardy-Weinburg equilibrium.
- There was no significant year-to-year variability in allelic frequency distribution in any population. All analyses were performed with sample years both separated and pooled.
- All of the 5 study populations were significantly differentiated based on Fst values (Table 3). The range of values was 0.0112-0.0570 (pooled years).
- No evidence of bottlenecked populations.
- The caldera populations (Surprise Lake and Aniakchak River Above Gates) were more reproductively isolated from Albert Johnson Creek (Fst=0.0427 and Fst=0.0385) than Black Lake (Fst=0.0184 and Fst=0.0200) (pooled years).

Conclusions

These results depict unexpected relationship between lake-type and river-type sockeye populations (Fig. 2). We expected Albert Johnson Creek sockeye to be the most closely related population to the recently-colonized caldera populations. These data show, to the contrary, Albert Johnson Creek to be more isolated than the geographically distant Black Lake.

The absence of year-to-year variability and lack of recent bottleneck evidence in the caldera populations suggest that these populations probably persisted through the 1931 eruption event. Alternatively, consistent gene flow since recolonization could erase such evidence

The close genetic relationship of Meshik Lake sockeye (Bering Sea drainage) to all other study populations (Pacific drainages) mirrors the geographic proximity from a terrestrial perspective. However, this is in stark contrast with the great ocean migratory distance of the drainages (1,200 km), and suggests the possibility of past connection with the Aniakchak drainage. During the breach of the caldera wall and catastrophic flood, the Meshik drainage may have been redirected from a Pacific drainage to the Bering Sea. More genetic analyses with other populations on the Bering Sea side of the Peninsula are necessary for substantial support or disproof of this hypothesis.

The two caldera spawning groups (SL and ARAG) are the closest related populations in this study, yet are still significantly differentiated and spawn in different habitats. Since genetic and morphological (Troy Hamon, unpublished data) differences exist in the spawning adults we may be witnessing a developing case of ecological speciation.

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